



WILEY

Elk Habitat Use Relative to Forest Succession in Idaho

Author(s): Larry L. Irwin and James M. Peek

Source: *The Journal of Wildlife Management*, Vol. 47, No. 3 (Jul., 1983), pp. 664-672

Published by: Wiley on behalf of the Wildlife Society

Stable URL: <https://www.jstor.org/stable/3808602>

Accessed: 14-02-2019 21:39 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

Wildlife Society, Wiley are collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management*

ELK HABITAT USE RELATIVE TO FOREST SUCCESSION IN IDAHO

LARRY L. IRWIN, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071
JAMES M. PEEK, Department of Wildlife Resources, University of Idaho, Moscow, ID 83843

Abstract: Home range use and habitat selection by a nonmigratory elk (*Cervus elaphus*) herd in relation to forest succession in the cedar-hemlock (*Thuja-Tsuga*) zone of northern Idaho were studied through use of radiotelemetry. In spring, elk preferred grass-shrub and seral shrub successional stages for feeding and tall seral brushfields or pole-timber stands for resting. Elk fed in clear-cuts and seral shrub communities in summer and rested primarily within pole-timber stands on ridges. In autumn, elk shifted to pole-timber communities on mesic slopes. No significant selection patterns occurred on winter range. Elk preferred to rest in areas over 400 m from traveled roads in all seasons. Home ranges contained more foraging area (35 vs. 20%) and less thermal and hiding cover (64 vs. 79%) than present in the study area overall. Selection of home ranges was related to forage production in seral stages of succession. Cover and human disturbance were important in habitat use in autumn.

J. WILDL. MANAGE. 47(3):664-672

The cedar-hemlock zone in northern Idaho and adjacent areas is managed primarily for timber products, but is also productive for big game populations that increased after wildfires in the early decades of this century. Advancing forest succession produced declines in habitat quality (E. R. Norberg and L. Trout, unpubl. rep., Idaho Dep. Fish and Game Fed. Aid Proj. W-112-R, 1957; Leege 1969), which, coupled with a national need for more intensive forest management, place a paramount need for details on big game-habitat interactions. Accordingly, Scotter (1980) and Lyon and Jensen (1980) concluded that the availability of habitats that support palatable forage and the manner in which big game select home ranges and exploit resources within home ranges are critical to management.

A knowledge of habitat preferences is needed for each successional complex, because North American cervids occupy a wide range of habitats and have been classified as generalist herbivores. Their diets vary according to availability of palatable forage (Bergerud 1972, Kufeld et al. 1973, Belovsky 1978). Recent procedures for big game habitat evaluation for the Blue Mountains of Oregon and Washington (Black et al. 1976, Thomas 1979), and for

other western states predict big game responses to changes in the ratio of cover to forage created through forest management. However, these guidelines are incomplete because they describe big game responses immediately after logging and do not account for relative differences in the value of different successional stages. The objectives of this study were to relate habitat selection by elk to physiography, forest stand structure, and understory production within a mosaic of communities representing the successional sequence in the cedar-hemlock zone in the Idaho panhandle.

We thank the Intermountain Forest and Range Experiment Station, U.S. Forest Service; University of Idaho; Idaho Fish and Game Department; Idaho Panhandle National Forest; and the Pope and Young Club for support. We especially thank W. D. Carrier and M. Schlegel for flight time and help in trapping. Field assistance was provided by H. L. Allen, L. A. Krone-mann, and W. T. Wittinger.

STUDY AREA

The study was conducted along the Coeur d'Alene River, where elevations range from 850 to 1,900 m. The area receives over 120 cm of annual precipitation

and snow often accumulates in depths over 100 cm. Weather patterns during the study were normal, except that precipitation in winter 1976–77 was only 50% of normal.

We recognized 3 major, somewhat interspersed vegetation zones: pine–fir (*Pinus–Pseudotsuga*) up to 950 m, cedar–hemlock for 850 to 1,600 m, and spruce–fir (*Picea–Abies*) above 1,500 m. Climax vegetation associations, or habitat types, were mainly western hemlock (*Tsuga heterophylla*)–myrtle pachistima (*Pachistima myrsinites*) on 74% of the area and grand fir (*Abies grandis*)–myrtle pachistima on 16% of the area. Habitat types of the spruce–fir zone (8% of the area) included overstories of mountain hemlock (*T. mertensiana*) or subalpine fir (*Abies lasiocarpa*) mixed with Engelmann spruce (*Picea engelmannii*). The remaining 2% of the study area was within the Douglas-fir (*Pseudotsuga menziesii*)–mallow ninebark (*Physocarpus malvaceus*) habitat type on steep breaks adjacent to major streams. Those types are more completely described by Daubenmire and Daubenmire (1968).

Old-growth western hemlock and western white pine (*Pinus monticola*) up to 1.5 m diameter and >85% canopies (Irwin and Peek 1979a) composed about 28% of the area. The remainder of the area was a mosaic of successional stages created by a series of large wildfires in 1910, 1919, 1926, and 1931. Mesic sites burned in the 1910 fire were in a late seral, mature tree stage that occupied 14% of the area. About half of the area burned in 1910 was again burned in 1931 and was mainly covered by dense pole-timber (>80% canopy) that was usually less than 25 cm in diameter. Drier slopes and ridge spurs were covered by dense brushfields of snowbrush ceanothus (*Ceanothus velutinus*) and/or Scouler willow (*Salix scouleriana*). Steep breaks supported a grass–shrub community that included elk sedge (*Carex gey-*

eri) and bluebunch wheatgrass (*Agropyron spicatum*) interspersed with scattered shrubs such as mallow ninebark and Saskatoon serviceberry (*Amelanchier alnifolia*). Another successional stage was created by logging, including clear-cuts 3–15 years of age that comprised 7% of the area.

METHODS

We sampled vegetational cover and production to relate habitat use to understory conditions using 20 20 × 50-cm plots spaced 5 m apart within 5 stands of each of 5 major successional stages: grass–shrub, seral brushfield, clear-cut, pole-timber, and mature/old-growth. Mature and old-growth timber stands were treated as 1 stage due to similarities in understories. Ten additional clear-cuts and 10 additional mature/old-growth stands were sampled to determine differences due to aspect. Significant differences ($P < 0.05$) among successional stages and aspects for shrub and forb cover and for oven-dried forb biomass were determined by analysis of variance. Physical descriptions, recorded in 20 stands of each of the 5 successional stages, included average tree height and density (estimated) and percent canopy closure determined with a spherical densiometer (Lemmon 1957).

Habitat use was evaluated using radiotelemetry. Free-ranging elk were immobilized, fitted with plastic 164-MHz transmitter collars (Pedersen 1977), and monitored with 3-element Yagi antennae from an airplane or by ground triangulation. An extensive road system provided access to receiving stations and usually allowed approach within 400–600 m of the elk to maximize accuracy of radiolocations without causing alarm. Use of habitats was measured within a 1-ha circle around each radiolocation.

Availability of habitat components was measured by describing random points (Marcum and Loftsgaarden 1980) and us-

Table 1. Average forb biomass, forb cover, and shrub cover in 5 successional stages, Idaho Panhandle National Forest, 1975–77.

Clear-cut			Shrub	Grass-shrub	Pole-timber	Mature/old-growth		
North ^a	East ^a	South ^a				East ^a	South ^a	North ^a
Forb biomass (g/m ²)								
245.4 ^b	117.8 ^c	69.4 ^c	44.6	31.9	26.5	29.8	20.2	13.6
Forb cover (%)								
57.6 ^b	50.2 ^b	28.5	28.6	22.0	31.7	43.5 ^b	31.8	27.4
Shrub cover (%)								
9.3	17.5	15.5	74.4 ^b	23.4	34.7 ^c	13.8	12.8	5.1

^a Aspect.
^{b,c} Different ($P < 0.05$) from other values in row that do not have the same superscript.

ing a digitizing planimeter. Data were stratified by season and daily periods, because observations and telemetry indicated elk fed most actively in the early morning or late afternoon–evening periods. Chi-square analyses and a Bonferroni z -statistic (Neu et al. 1974) were used to determine preference or avoidance as indicated by differences ($P < 0.05$) between use and availability. To test for differences among individuals, we also compared use and availability within home ranges for habitat type, successional stage, and aspect. Home ranges were mapped according to the modified minimum home area method (Hayne 1949) and compared to the study area according to the criteria of Black et al. (1976): hiding cover included cover capable of hiding elk at 61 m or less, thermal cover included coniferous cover ≥ 12 m tall and at least 70% canopy closure, and forage area included all area not in cover but excluded nonproductive areas such as roads or rock outcrops. Only mature and old-growth stands qualified as thermal cover, whereas most coniferous stands fit the definition of hiding cover.

RESULTS

Vegetation Analyses

The 5 successional stages differed in understory production (Table 1). Clear-

cuts produced prolific forb and shrub complexes. Those on north and east aspects were most productive of forb biomass and cover. Seral brushfields produced the largest amounts of shrub cover, but grass-shrub and pole-timber types were also productive of shrubs. Shrub species composition varied, however, as tall shrubs predominated in seral brushfields and grass-shrub types. Low shrubs, primarily myrtle pachistima, provided the major understory cover in pole-timber stands.

Radiotelemetry Data

Sixteen elk were radio-marked, including 2 yearling bulls, 2 2-year-old bulls, 1 yearling cow, and 11 adult cows. Five cows were monitored for 3 years and 2 others for 16 months. We obtained 1,443 relocations, with 44% occurring in summer when access was best. Most locations occurred from 0300 to 2100 hours. Eight animals were each located over 70 times and 1 was located over 200 times. Statistically valid information was gathered for only 2 of the 4 bulls, precluding separation of data by sex. These elk were not migratory; annual movements were less than 20 km and averaged only 5 km. The lack of migration provided an opportunity to compare habitat preferences within home ranges and within the study area.

Spring Habitat Selection: 21 April–15 June

We recorded 384 relocations in spring, including 196 during morning–evening activity periods and 188 during resting periods. Elk preferred to feed in grass–shrub and shrub successional stages in the grand fir habitat type. The western hemlock habitat type received the major share of the use, but use was not greater than availability (70 vs. 76%). Preferred areas contained the following characteristics: forest canopies <25% and <650 trees/ha, gentle slopes or ridges at low elevations and 200–400 m from water, and areas <200 m from a large opening. Initiation of vegetative growth in these areas was early, and they contained salt licks used primarily in spring.

Elk usually returned to higher elevations by mid-morning to rest in areas over 400 m from traveled roads. These areas included tall brushfields or sparse pole-timber with trees less than 12 m tall (Fig. 1) and with 50–75% canopy closure, west aspects, ridges, and ridge spurs. However, they remained less than 200 m from openings.

Individual variation in habitat use within home ranges in spring was marked. The sample of marked animals preferred south or west slopes within the grand fir–myrtle pachistima habitat type; only 1 elk indicated preference for this type in its home range. Over 88% of the locations of 2 elk were in western hemlock–myrtle pachistima; 1 preferred it. Thus, use of areas in the grand fir type was coincidental to selection of exposed slopes and seral stages of succession. One elk preferred clear-cuts, 3 preferred grass–shrub types, and 2 preferred shrubfields for feeding. They avoided dense coniferous timber, and over 80% of the locations of 3 elk consistently using clear-cuts for feeding were within 400 m of a road. However, vehicle activ-

ity on the access roads was negligible in spring.

The pattern of spring habitat use within home ranges was for selection of habitats that produced large quantities of succulent, early-growing forage such as found in clear-cuts, grass–shrub communities, or seral brushfields. Track counts in clear-cuts indicated elk most often entered those feeding areas from adjacent coniferous cover uphill. Minor differences among years resulted from variations in snow-melt and phenology of forage. Mid-elevation clear-cuts were used more often in 1977, when initiation of vegetative growth was early. Areas used by radio-marked elk during calving were highly variable among individuals and years, and no concentrated calving grounds were observed.

Summer Habitat Selection: 16 June–8 September

We obtained 644 relocations in summer, including 340 when elk were active and 304 during resting periods. During active periods, the marked animals collectively indicated preference for the grand fir type in the seral shrub stage of succession. Areas within the western hemlock type received the most use, but use was similar to availability (72 vs. 76%). This coincided with selection for areas near openings on gentle ridges with sparse timber at intermediate elevations. Many elk were observed feeding in clear-cuts, but elk generally used clear-cuts in proportion to availability (Fig. 1). They preferred ridges with pole-timber stands that produced 50–75% canopy closure in areas greater than 400 m from a traveled road during resting periods.

Although the radio-marked elk preferred areas in the grand fir type, some home ranges contained little area within that habitat type. One elk preferred western hemlock, another preferred clear-cuts, 3 preferred shrubfields, 1 preferred pole-

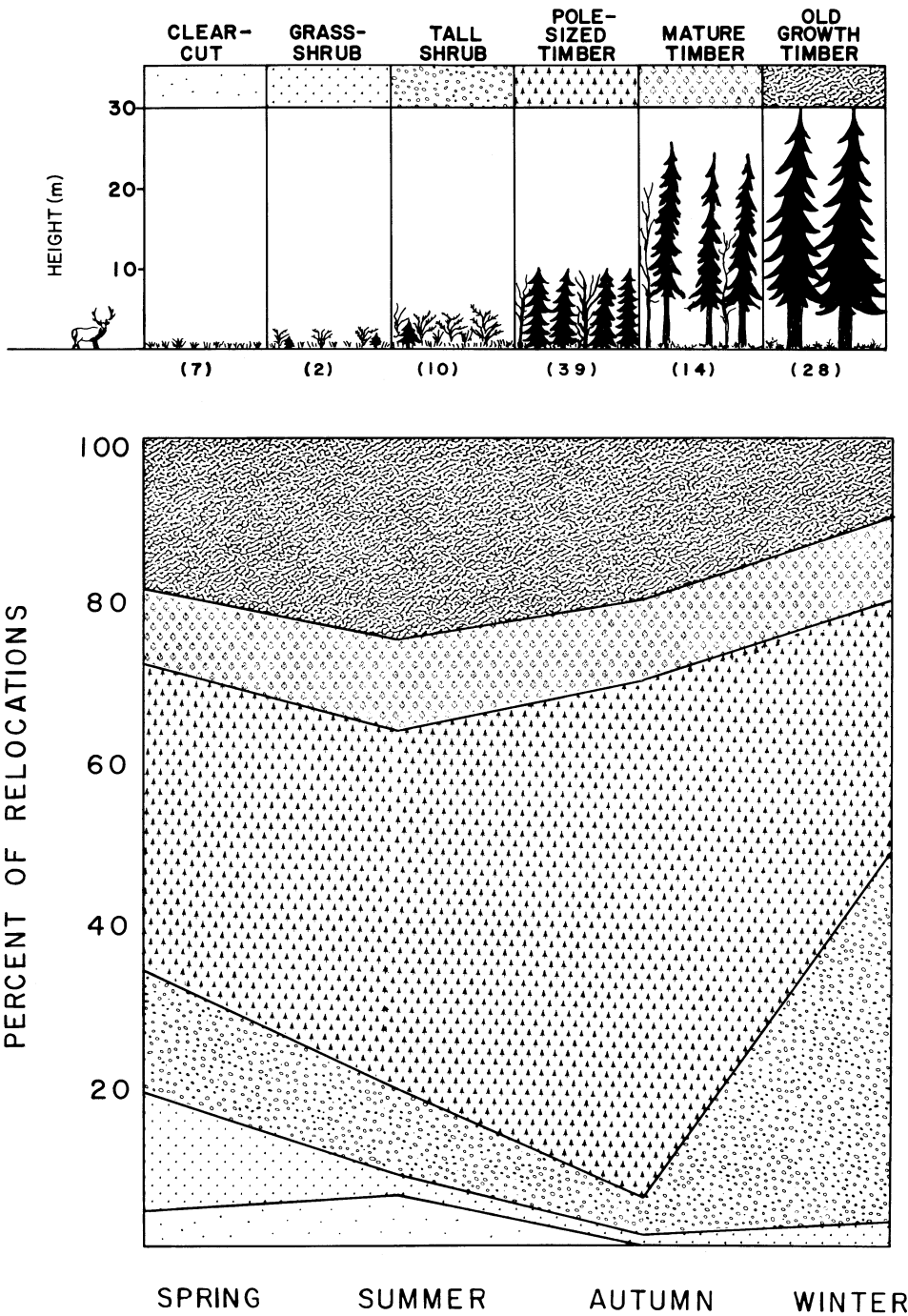


Fig. 1. Percentages of radiolocations of elk within successional stages in the cedar-hemlock zone of northern Idaho. Numbers in parentheses indicate percentage of study area occupied by each successional stage.

timber, and 2 preferred mature timber and old-growth. Three elk avoided areas in the grass-shrub successional stage within their home ranges. Two pairs of elk that shared nearly common home ranges used their home ranges in similar manners. The habitat use pattern within home ranges included use of areas that produced the largest amounts of succulent forbs or shrubs in north- or east-facing clear-cuts interspersed within old-growth forest, or brushfields within 2nd-growth forest.

Autumn Habitat Selection: 9 September–20 December

We located radio-marked elk 269 times in autumn, with 8 animals providing most of the data. Habitat selection patterns were distinct from those in spring and summer, and there were fewer differences between active and resting periods. Elk preferred pole-timber (Fig. 1) with greater than 75% canopy closure in the western hemlock type, and avoided the grand fir and subalpine fir habitat types. Elk preferred gently sloping ridges and spurs but avoided south exposures. Vehicle activity on mountain roads increased and elk preferred to be greater than 400 m from traveled roads at all times, and 400–600 m from openings larger than 1 ha. Ninety-five percent of the locations were within 400 m of water, coinciding with a decrease in use of higher elevations. Old-growth timber was used proportionately less than its availability, but late in autumn we observed increased use of old-growth at lower elevations where green forage was still available under dense canopies that intercepted most of the early snowfall.

Much less variation in habitat use within home ranges occurred among individuals in fall. Few radiolocations occurred in the mountain hemlock or subalpine fir types, because elk using home ranges con-

taining those types moved to lower elevations. All elk increased use within the western hemlock type. Five of 8 intensively monitored elk preferred north or east aspects, coinciding with selection for dense pole-timber stands that were more prevalent on those slopes and for sites close to water. There was little use of clear-cuts, grass-shrub types, or seral brushfields, probably because forage had become dry in those successional stages. During the autumnal shift in habitat use, females did not leave home ranges but 3 young bulls moved to distinctly new areas.

Winter Habitat Use: 21 December–20 April

Most of the elk winter ranges within the Coeur d'Alene River drainage were in areas burned in the large fires in 1910, 1919, and 1931. During the 2 winter periods of study, we obtained 146 radiolocations. Low sample sizes precluded stratification into daily periods, and only a few significant preferences were found. All radio-marked elk shared the same winter range, which was almost entirely within differing stages of secondary succession following the 1931 wildfire and included tall brushfields interspersed with pole-timber (Fig. 1) on north slopes and ridge spurs.

Elk used the following features in proportion to availability: habitat type, successional stage, canopy cover, elevation, and distance to an opening. However, observations showed that elk frequently used dense stands of lodgepole pine (*Pinus contorta*) and western hemlock for resting, especially at night, and that they also bedded under tall willow clumps on south exposures. Rather than selecting components within the winter range, elk apparently selected a southwest-facing home range with an adequate supply of forage and cover. During the

latter part of winter 1976–77, more snow-free areas were available and elk moved to adjacent grass-shrub and sparse timber stands for feeding.

Home Ranges

Radio-marked elk concentrated activities in home ranges away from low-elevation logging roads and the paved road along the river. Twelve elk selected home ranges entirely within areas burned since 1900, 2 were mostly in old burns and old-growth, and 2 were almost entirely in old-growth interspersed with clear-cuts. Spring-fall home ranges averaged 1,259 ha, but 6 cows with calves had summer ranges of 820 ha and the ranges of 2 yearling bulls were slightly smaller. Fall home ranges were reduced (840 ha), and the common wintering area was only 210 ha in size. Spring-fall home range sizes seemed related to habitat components: the largest were composed of larger proportions of mature and old-growth timber where most clear-cuts occurred. Home ranges generally contained less mature and old-growth timber than the study area (23 vs. 42%), and more pole-timber and grass-shrub communities (54 vs. 41%). Seral brushfields and clear-cuts were included in proportion to their occurrence in the study area. Home ranges averaged 35% forage area, 24% thermal cover, and 40% hiding cover, whereas the study area contained 20, 45, and 34%, respectively.

All but 1 of 7 elk monitored for more than 1 year had high fidelity for seasonal home ranges each year. In 1977, 1 adult cow used 2 alternate summer home ranges separated by a distance of 16 km: 1 in pole-timber with exposed slopes in a seral shrub stage and 1 within a large 25-year-old brushy clear-cut.

DISCUSSION

Elk occur in a broad variety of habitats across their range in North America, in-

dicating a niche-generalist life strategy as contrasted with many African ungulates (Wilson and Hirst 1977). However, of the 4 levels of habitat selection recognized by Johnson (1980), we observed 3 that occur locally among elk: selection of a home range, seasonal selection within a home range, and differences in selection among daily periods.

Home ranges appear to be established first, as they were clearly defined by mid-summer. Elk explored food and cover patches, even during periods of concentrated use. When food patches were abundant and productive, elk reduced exploration, a situation also observed by Miller (1970) for black-tailed deer (*Odocoileus hemionus columbianus*). Once familiarity occurred, exploration ceased, because elk show high fidelity to seasonal home ranges (Knight 1970, Craighead et al. 1972).

Forage conditions, including at least forage density and phenology in seral stages of succession, appear to be key factors influencing size and location of home ranges. This supports data reported by Clary and Larson (1971) and Franklin et al. (1975), who correlated frequency of elk use with forage abundance. This relationship probably is stronger than we observed, because radiotelemetry observations may underestimate the value of better foraging habitats where elk presumably would spend less time filling rumens. Social relationships and population density, not evaluated in this study, probably are also important in home range selection. Shelter and human disturbance appear to be secondary factors.

Daily and seasonal habitat selection within home ranges is strongly influenced by phenology and productivity of forage in grass-shrub communities in spring, clear-cuts or seral brushfields in summer, and dense pole-timber on mesic slopes in fall. Pole-timber stands provide better escape cover than mature/old-

growth due to lower limbs and greater tree density. These secondary levels of selection are influenced by human disturbances on forest roads (Lyon 1979), by topography, and probably by social and physiological phenomena associated with breeding. In winter, elk did not select habitats within a home range, as also observed by Schoen (1977). Instead, they selected the same, westerly exposed, small home range in an early successional stage. Moen (1973:267) noted that early stages of forest succession, including the shrub stage, may provide thermal cover as effectively as a dense canopy, because they reduce convective heat losses. Because no selection occurred within the winter range, habitat selection based upon forage supplies in other seasons may be adaptive in deep snow areas, especially where winter forage rapidly deteriorates through forest succession.

MANAGEMENT IMPLICATIONS

Many timber stands supply both forage and cover for elk. Old growth and mature timber, classified as both thermal and hiding cover, were used proportionately less than availability in fall, and elk preferred dense pole-timber stands that produced more palatable forage. Home ranges contained proportionately more foraging area and less thermal cover than occurred in the study area, but some forage areas were used for only part of the year, becoming less used as forage became dry. Instead of forage-cover prescriptions, biologists need to discover which successional stages are most productive of forage and cover, and which are preferred at each season.

Judicious logging to create a series of successional stages will improve elk habitat in the cedar-hemlock zone. Track counts indicated that 14–20-ha clear-cuts were used most. Adequate cover (over 75% canopy) adjacent to foraging areas should be maintained in pole-timber stands over

24 ha in size when roads remain open (Irwin and Peek 1979a). South or southwest slopes adjacent to major drainages and near known winter ranges could be logged and broadcast-burned to produce tall shrubs, potentially useful as winter range within 15–20 years (Irwin 1976, Irwin and Peek 1979b). Some old-growth forest adjacent to fall and winter ranges may be useful for forage use in late fall.

LITERATURE CITED

- BELOVSKY, G. E. 1978. Diet optimization in a generalist herbivore: the moose. *Theor. Pop. Biol.* 14:105–134.
- BERGERUD, A. T. 1972. Food habits of Newfoundland caribou. *J. Wildl. Manage.* 36:913–923.
- BLACK, H. C., R. J. SCHERZINGER, AND J. W. THOMAS. 1976. Relationships of Rocky Mountain elk and Rocky Mountain mule deer habitat to timber management in the Blue Mountains of Oregon and Washington. Pages 11–13 in J. M. Peek and S. R. Hieb, eds. *Proc. Elk-logging-roads Symp.*, Univ. Idaho For., Wildl., and Range Exp. Stn., Moscow.
- CLARY, W. R., AND R. R. LARSON. 1971. Elk and deer use are related to food sources in Arizona ponderosa pine. U.S. Dep. Agric., For. Serv. Res. Note RM-202. 4pp.
- CRAIGHEAD, J. J., G. ATWELL, AND B. W. O'GARA. 1972. Elk migration in and near Yellowstone National Park. *Wildl. Monogr.* 29. 48pp.
- DAUBENMIRE, R. F., AND J. B. DAUBENMIRE. 1968. Forest vegetation of eastern Washington and northern Idaho. *Wash. State Univ. Agric. Exp. Stn. Tech. Bull.* 60. 104pp.
- FRANKLIN, W. L., A. S. MOSSMAN, AND M. DOLE. 1975. Social organization and home range of Roosevelt elk. *J. Mammal.* 56:102–118.
- HAYNE, D. W. 1949. Calculation of size of home range. *J. Mammal.* 20:1–18.
- IRWIN, L. L. 1976. Effects of intensive silviculture on big game forage sources in northern Idaho. Pages 135–142 in J. M. Peek and S. R. Hieb, eds. *Proc. Elk-logging-roads Symp.*, Univ. Idaho For., Wildl., and Range Exp. Stn., Moscow.
- , AND J. M. PEEK. 1979a. Relationships between road closures and elk behavior in northern Idaho. Pages 199–204 in M. S. Boyce and L. D. Hayden-Wing, eds. *North American elk: ecology, behavior, and management.* Univ. Wyoming, Laramie.
- , AND ———. 1979b. Shrub production and biomass trends following five logging treatments in the cedar-hemlock zone of northern Idaho. *For. Sci.* 25:415–426.
- JOHNSON, D. H. 1980. The comparison of usage

- and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- KNIGHT, R. R. 1970. The Sun River elk herd. *Wildl. Monogr.* 23. 66pp.
- KUFELD, R. C., O. C. WALLMO, AND C. FEDDEMA. 1973. Foods of the Rocky Mountain mule deer. U.S. Dep. Agric., For. Serv. Res. Pap. 111. 31pp.
- LEECE, T. A. 1969. Burning seral brush ranges for big game in northern Idaho. *Trans. North Am. Wildl. and Nat. Resour. Conf.* 34:429–438.
- LEMMON, P. E. 1957. A new instrument for measuring forest overstory density. *J. For.* 55:667–669.
- LYON, L. J. 1979. Habitat effectiveness as influenced by roads and cover. *J. For.* 77:658–660.
- , AND C. E. JENSEN. 1980. Management implications of elk and deer use of clear-cuts in Montana. *J. Wildl. Manage.* 44:352–362.
- MARCUM, C. L., AND D. O. LOFTSGAARDEN. 1980. A nonmapping technique for studying habitat preferences. *J. Wildl. Manage.* 44:963–968.
- MILLER, F. L. 1970. Distribution patterns of black-tailed deer (*Odocoileus hemionus columbianus*) in relation to environment. *J. Mammal.* 51:248–260.
- MOEN, A. N. 1973. Wildlife ecology: an analytical approach. W. H. Freeman and Co., San Francisco, Calif. 458pp.
- NEU, C., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541–545.
- PEDERSEN, R. 1977. Big game collar-transmitter package. *J. Wildl. Manage.* 41:578–579.
- SCHOEN, J. W. 1977. The ecological distribution and biology of wapiti (*Cervus elaphus nelsoni*) in the Cedar River watershed, Washington. Ph.D. Diss., Univ. Washington, Seattle. 405pp.
- SCOTTER, G. W. 1980. Management of wild ungulate habitat in the western United States and Canada: a review. *J. Range Manage.* 33:16–27.
- THOMAS, J. W., Editor. 1979. Wildlife habitats in managed forests—The Blue Mountains of Oregon and Washington. U.S. Dep. Agric., For. Serv. Handb. 533. 512pp.
- WILSON, D. E., AND S. M. HIRST. 1977. Ecology and factors limiting roan and sable antelope populations in South Africa. *Wildl. Monogr.* 54. 111pp.

Received 21 April 1982.

Accepted 4 August 1982.